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REVIEW

Spider locomotion on the water surface: biomechanics and diversity

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Abstract. Spiders in many families are capable of locomotion on the surface of water, a capability that, at its simplest, requires only a strongly hydrophobic integument and the same postures and motions that are used on land. Specialized aquatic gaits, in contrast, are only characteristic in the Pisauridae, Trechaleidae, Ctenidae, and Tetragnathidae. They are less common features of aquatic locomotion in Lycosidae, are only occasionally encountered in Salticidae, and are rare in Araneidae. Most of what is known about the biomechanics of these specialized gaits comes from research on fishing spiders (Pisauridae) and, because the physics and hydrodynamics are similar in many respects, on water striders (Insecta: Hemiptera: Gerridae). In what follows, I have concentrated on the biomechanics of propulsion in water-walking spiders and water striders because propulsion on the air-water interface was mysterious until the 1990s when researchers began seeking answers to the central question: What provides the resistance against which a spider or water strider pushes when it sweeps its legs backward? The answers, now nearly complete, include a) dimple distortion, b) drag, c) generation of vortices, and d) nanoscale brushing of the water surface by hydrophilic hairs.

Keywords: Aquatic propulsion, air-water interface, hydrophobic surface, nanoscale, gait, rowing, galloping, phylogeny, performance, fishing spiders, water striders

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1. INTRODUCTION

The surface of a pond or stream is an interface between air and water. The surface itself is in tension and thus is capable of supporting an organism that is denser than the underlying water. And the underlying water, being both dense and somewhat viscous, resists local changes in its momentum, making it possible for an organism to push against the water and thus propel itself (Denny 1993; Vogel 1994).

A number of organisms make use of this peculiar environment, some just passing through the way an aquatic mite does when quitting its submerged existence (Meyer 1985) and others, like water boatmen (Hemiptera: Corixidae: Hinton 1976), refreshing the oxygen they use in plastron respiration (Flynn & Bush 2008). For some, though, like water striders and fishing spiders (Fig. 1), the interface is their primary (if not necessarily their obligate) physical substrate, supporting communication, predation, and locomotion (Wilcox 1979a, b; Foelix 2011).

My purpose in the following pages is to consider walking on water by arthropods, particularly spiders but also water striders (Heteroptera: Gerridae), paying attention throughout to the relationships between structure and function.

2. PERFORMANCE

2.1 Gaits.—Spiders in a wide variety of families are capable of effective locomotion on the water surface (Ehlers 1939; Shultz 1987; Barnes and Barth 1991; Suter et al. 2003; Stratton et al. 2004). This locomotion can take the form of walking or running with the same stepping gait as is seen on solid ground (Shultz 1987) or can involve altogether different gaits, presumably honed by natural selection, that function effectively on the water surface. Three qualitatively distinct water-surface gaits have been identified (Table 1).

Thus there are really four major gaits used by spiders on the water surface: 1) walking with the alternating tetrapod

Figure 1.—*Dolomedes triton*, a fishing spider (Pisauridae), and *Gerris* sp., a water strider, at rest on the water surface. The spider's weight is borne primarily by the distal parts of its legs where they push down on the water surface forming visible dimples there. The ventral surface of the prosoma also presses on the water surface as indicated by the dimple under that part of the spider. The water strider's weight is borne entirely on the ends of its six legs.

locomotion that is characteristic of spiders on solid substrates, 2) rowing, using pairs of contralateral legs in synchrony, 3) crawling, using the first pair of legs in alternation and 4) galloping, in which downward and backward thrusts of the first three pairs of legs produce strings of leaps from the water surface. Videos of the aquatic locomotion of a rowing and galloping *Dolomedes triton* (Walckenaer, 1837), a crawling *Tetragnatha* spp., a rowing salticid, and a walking *Geolycosa rogersi* Wallace, 1942 (a lycosid that does not have a gait specialized for use on the water surface), are available online at http://www.bioone.org/doi/suppl/10.1636/M13-14.

2.2 Velocity.—The velocity of water-surface locomotion has been measured in only a few species of spiders, with a concentration on the nursery web or fishing spiders (Pisauridae). Suter et al. (2003) compared gaits and velocities of spiders in seven families (Fig. 2), finding that galloping fishing spiders (Pisauridae) had by far the highest absolute velocities (mean > 0.4 m/s), but that among spiders with gaits that had no aerial phase, *Tetragnatha* sp. (Tetragnathidae) using the "crawl" achieved both the highest absolute and relative velocities (0.25 m/s, 29 body lengths/s). Hu and Bush (2010) reported fishing spiders rowing at a mean velocity of 0.15 m/s and galloping at 0.35 m/s.

Suter and Gruenwald (2000a) measured rowing velocities achieved by many sizes of the fishing spider, *Dolomedes triton*: spiders spanning a 600-fold range of masses could all row at about the same velocity (mean = 0.11 m/s), with the largest variation occurring at the very smallest sizes. In terms of relative velocity, however, largely because of the increase in stride frequency with decreasing mass, the smallest spiders rowed at about 42 body lengths per second while the largest spiders only achieved about 6 bl/s.

2.3 Efficiency.—For most spiders that frequent the water surface, we lack estimates of the efficiency of the gaits used (but see Brown & Formanowicz 2012). However, in *Dolomedes* (Pisauridae), Hu and Bush (2010) calculated locomotion efficiency using the Strouhal number (*St*), the dimensionless ratio of the product of stroke frequency and stroke amplitude to forward velocity, as 0.3 for rowing and 0.4 for galloping. These are close to what is found for swimming in fish of all sizes (0.25 to 0.35; Denny 1993; Vogel 1994, 2013), for the fastest water-walking insects, water striders (Gerridae, 0.2; Hu and Bush 2010) and for birds in flapping flight (Taylor et al. 2003). Taylor et al. (2003) have argued that natural selection on fluid-based locomotion efficiency (i.e., in air and water) has constrained animals to the range of *St* expected for high propulsive efficiency, $0.2 < \mathrm{St} < 0.4$.

More interesting in the current context would be comparisons of locomotion efficiency in spiders of about the same size that use a terrestrial gait on water vs. ones that use a specialized aquatic gait. This would be readily possible between selected members of Lycosidae and any of the Pisauridae (Stratton et al. 2004).

3. PHYLOGENETIC DISTRIBUTION

Locomotion on the water surface, supported there not by buoyancy but by surface tension or by hydrodynamics, is uncommon but has apparently evolved independently many times in the animal kingdom. Bush and Hu (2006) count more than 1200 species that either habitually or in extremis propel themselves across the water surface, including mammals, birds, reptiles, fish, insects and spiders. Among spiders, the fishing spiders (Pisauridae) (Fig. 1) are best known and may be the most adept at this form of locomotion (below), but they are by no means alone.

In the most extensive compilation of information on water-surface locomotion in spiders, Stratton et al. (2004) surveyed the capabilities of nearly 250 spider species in 42 families. In each species, they looked both at the interaction between the water surface and the spider's integument, where wettability (see 4.1.2) determines whether the spider is trapped by the water's adhesive properties or can exploit the water's surface tension, and at the spider's propulsive behavior, if any. They found 1) that many spiders had hydrophilic surfaces, either in part or in full, that rendered them incapable of escaping

Table 1.—Specialized gaits used by spiders on the water surface.

Name	Exemplar	Description	Notes	References
Row	*Dolomedes* (Pisauridae)	legs III and II (or II nd I for Araneidae), in that order, provide rowing propulsion, members of each pair sweeping in unison; stroke primarily in lateral plane and posteriad; continuous contact between spider and water surface; (named by analogy with the propulsion of rowboats)	characteristic in Pisauridae, Trechaleidae, Ctenidae; characteristic in some species in Lycosidae; occasional in Salticidae; rare in Araneidae; variants include legs I in propulsion	Barnes & Barth 1991; Suter et al. 2003; Stratton et al. 2004
Gallop	*Dolomedes* (Pisauridae)	legs III, II, and I, in synchrony; stroke primarily in vertical plane and posteriad; contact between spider and water only during power stroke; (named by analogy with the galloping of horses and other mammals)	characteristic in Pisauridae	Gorb & Barth 1994; Suter & Wildman 1999
Crawl	*Tetragnatha* (Tetragnathidae)	legs I, alternating, sweep to the side and posteriad; (named by analogy with the human crawl swimming stroke)	known only in Tetragnathidae where it is characteristic in many species	Suter et al. 2003; Stratton et al. 2004

water's adhesive attraction, but 2) that the remainder had largely hydrophobic surfaces and so were well supported by the water surface. Among those species that stayed dry and on top of the air-water interface, a few remained immobile unless prodded while most immediately moved away using gaits that varied between ungainly scrambling and coordinated walking, rowing, crawling, or galloping.

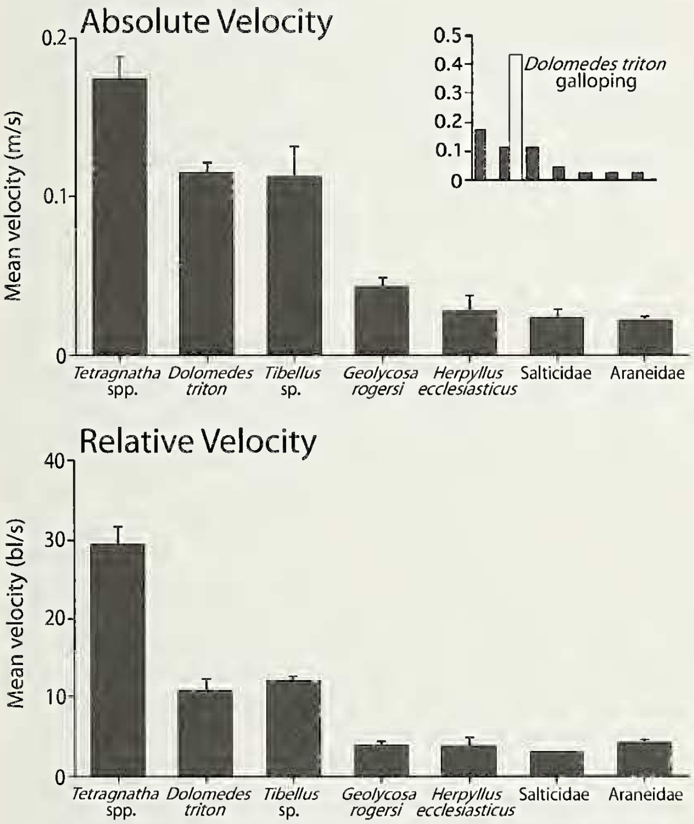

Figure 2.—Absolute and relative mean velocities of crawling, rowing or walking spiders, and galloping spiders (inset). By both absolute and relative (body lengths per second) measures, the long-jawed orb weavers (crawling; Tetragnathidae) were fastest. Velocities of *Dolomedes triton* (rowing; Pisauridae) and *Tibellus* sp. (walking; Philodromidae) were intermediate by both measures, but *D. triton* surpassed all others when galloping (inset). Adapted from Suter et al. 2003.

Although rowing, the gait on which Stratton et al. (2004) focused, was performed by a few orb weaving spiders (Araneidae) and a few jumping spiders (Salticidae), most of the rowing spiders were in the Grate-Shaped Tapetum clade (GST; Silva Davila 2003) (Fig. 3). There, rowing was found only in Lycosidae, Pisauridae, Trechaleidae, and Ctenidae. Stratton et al. (2004) argued that rowing on the water surface evolved four times in spiders: once in jumping spiders, once in orb-weavers, once in the branch of the lycosoids that includes Lycosidae, Pisauridae, and Trechaleidae, and once in Ctenidae. Their analysis also included the juxtaposition of rowing propensity and characteristic habitat—their conclusion in that realm was that "phylogeny is a stronger force than current selection pressures arising from habitat in determining whether members of a species are capable of rowing" (Stratton et al. 2004:72).

4. BIOMECHANICS OF LOCOMOTION

Locomotion on the water surface presents animals with two core problems. On land, the solid surface resists the downward push that gravity imparts to denser-than-air organisms, whereas the density and viscosity of water offer much less resistance to the downward push. Similarly, on land, macroscopically irregular surfaces and static friction oppose leg motions in the horizontal plane, allowing an organism to push itself forward, while on water friction/drag can be very low and any horizontal leg motions meet with comparatively little resistance. These constitute the support and propulsion problems, respectively. We will consider these separately even though, for spiders and other surface-dwelling arthropods, solutions to the two problems share the exploitation of surface tension.

4.1 Support.—When the fishing spider, *Dolomedes triton* (Pisauridae), is at rest on the water surface, its weight distorts the surface, forming "dimples" wherever the spider and the water meet (Fig. 1). The spider remains at the surface because the downward push of its weight is opposed by a combination of the upward push of surface tension, accounting for about two-thirds of the spider's weight, and the upward push of

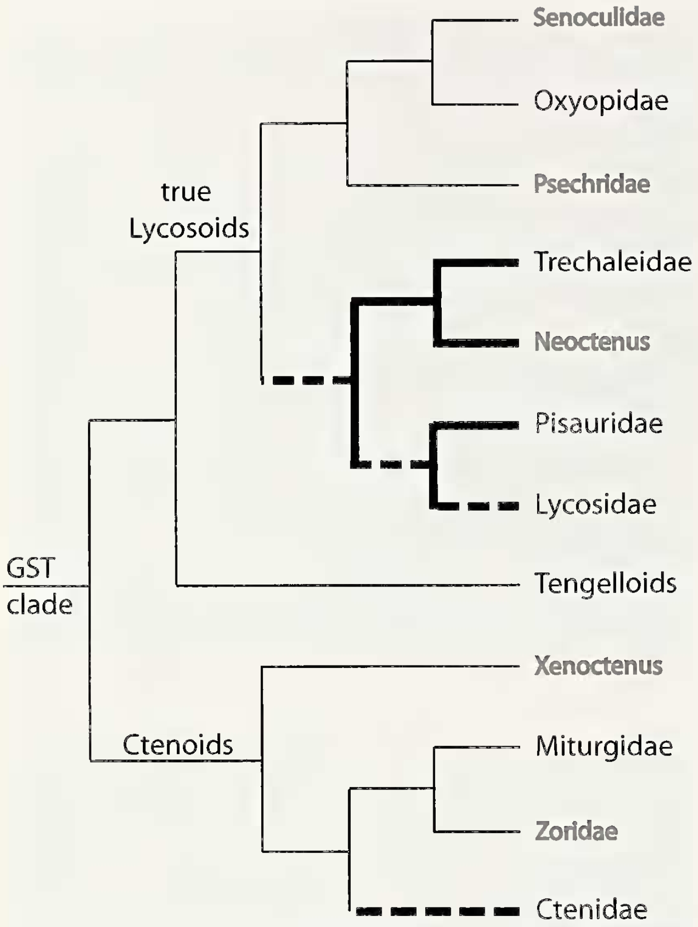

Figure 3.—A portion of the phylogenetic tree of spiders, showing the Grate-Shaped Tapetum clade that contains most of the spiders that use rowing as their characteristic gait during aquatic locomotion. Adapted from Stratton et al. 2004.

buoyancy accounting for the remaining one-third (Hu & Bush 2010). (This is one respect in which fishing spiders and water striders differ quantitatively: the water striders, being less massive and having comparatively thin legs, are supported almost entirely by surface tension, with buoyancy being negligible as a supporting force.) The legs and the undersides of the cephalothorax and abdomen remain dry (Stratton & Suter 2009). This relationship between nonwettable body parts and the malleable surface of water must be central in any discussion of water surface locomotion.

4.1.1 Properties of the water surface: The attributes of the air-water interface and their implications for organisms are clearly delineated in two well-known texts, *Air and Water: The Biology and Physics of Life's Media* (Denny 1993) and *Life in Moving Fluids: The Physical Biology of Flow* (Vogel 1994), and in a more recent review of locomotion on the water surface (Bush and Hu 2006).

The interface between water and air has a peculiar structure. Because water molecules are polar they are attracted to each other, giving water cohesion. The absence of comparable molecular interactions between water molecules and air molecules, that is, the absence of adhesion, means that the interface between the two fluids is relatively stable. Importantly for the current discussion, the cohesion between water molecules at the interface puts the water surface in tension, measured in units of force per distance (usually N/m). It takes energy or work to increase the exposed surface of the water, which means that the surface tension resists deformations such as those caused, for example, by the leg of a spider pushing down on the surface, or by any small wave or ripple.

In the context of support on the water surface, the air-water interface can be breached in two ways. If an appendage or other body part has a strongly hydrophilic surface, the water's surface tension provides no resistance and the appendage penetrates the surface unimpeded; if the part's surface is strongly hydrophobic, however, it cannot become submerged unless the downward force on it exceeds the upward resistance of the surface tension as it is applied along the perimeter of the contact area between the body part and the water surface. The degree to which these generalizations are true depends on the physical and chemical properties of the surface of the appendage (Bush et al. 2008).

4.1.2 Properties of spider surfaces: The species of spiders that most successfully exploit the water surface for locomotion have integuments rich in hairs that are themselves strongly hydrophobic (Suter et al. 2004; Stratton and Suter 2009; Foelix 2011). This coincidence of surface roughness (hairs, but also nano- and micro-scale unevenness) and molecular-level hydrophobicity (e.g., cuticular waxes) makes any surface impressively resistant to wetting (Wenzel 1936; Cassie and Baxter 1944; Quéré 2002, 2008). The two properties have been combined many times throughout biological evolution and are known to confer strong water repellency on both plants (Neinhuis and Barthlott 1997; Cerman et al. 2009) and animals, including insects (Holdgate 1955; Neville 1975; Gao and Jiang 2004) and spiders.

In the preceding two paragraphs, "hydrophobic" and "hydrophilic" appear to be the two parts of a dichotomy, whereas in fact they are categorical names for regions on a continuum. The continuum is defined by the ratio of the cohesion energy of water (its molecules' tendency to attract each other) and the adhesion energy where the water touches the solid substrate (the tendency of the water and solid molecules to stick together). Measuring the energies of cohesion and adhesion is difficult, but their ratio is easily measured because, as the ratio changes, so does the contact angle between the water and the solid surface (Young 1805; Denny 1993; Vella 2005; Bush et al. 2008). Water-walking arthropods have leg surfaces with contact angles that exceed 90°, above which the leg surface is nominally hydrophobic. The fishing spiders (147°, Stratton et al. 2004) and water striders (168°, Gao & Jiang 2004) have surfaces that are close to or above 150°, at which point they are often referred to as superhydrophobic (Bush et al. 2008).

Bush and his colleagues (Bush et al. 2008) summarized the interactions between arthropod integuments and water with a very useful combination of diagrams, photographs and mathematical models to augment their analyses. Because their review is both pertinent and nearly complete, it should be consulted by those interested in a more detailed summary than I have given above. More recently, Prakash & Bush (2011) showed that the orientation of surface roughness causes anisotropy (directionality) in the interactions of water and arthropod surfaces, an asymmetry that may be most

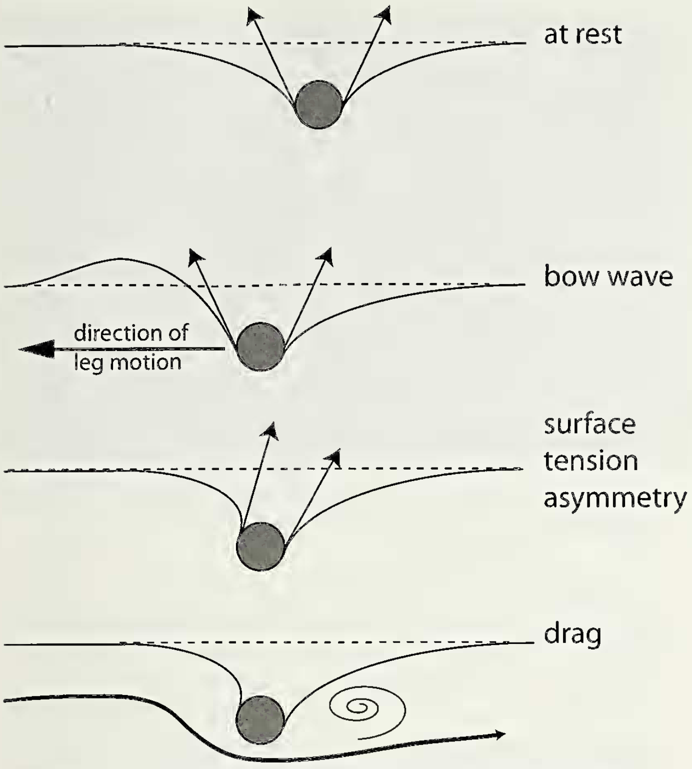

Figure 4.—Schematic representations of the relationship between the spider's leg (in cross section) and the dimple at rest (top) and during a rowing power stroke (bottom three). At rest, the curvatures of the sides of the dimple are symmetrical as are the directions of the vectors representing the forces on the leg due to surface tension. During a rowing power stroke, one or more of the three hypothesized sources of resistance to the leg's motion could be in play, as could brushing the water surface with hydrophilic hairs (not shown: see Hu & Bush 2010). Modified from Suter et al. 1997.

important for water-surface locomotion by very small spiders and water striders (see 4.2.1).

Having a strongly hydrophobic, hairy surface not only contributes to water-surface locomotion but also makes possible the physical lung with which submerged insects and arachnids can breathe (Crisp and Thorp 1948; Hinton 1976; Rovner 1986; Hebets and Chapman 2000; Flynn and Bush 2008; Balmert et al. 2011). Recent work confirms that the combination of hydrophobicity with hairiness or nanoscale roughness also renders a surface self-cleaning (Barthlott and Neinhuis 1997; Neinhuis and Barthlott 1997; Hiller 2009). In many spiders, this may currently be only one of its functions (Stratton and Suter 2009), but because hairy hydrophobicity was apparently a pre-adaptation to effective water-surface locomotion, its ancestral self-cleaning function may have been central.

4.2 Propulsion.—Spider locomotion on the water surface, like the locomotion of the better known water striders (Insecta: Gerridae), was well described before the mid-1990s but was not well explained; that is, the kinematics had been described (McAlister 1959; Anderson 1976; Bowdan 1978; Shultz 1987; Barnes and Barth 1991; Gorb and Barth 1994), but the mechanism of transfer of momentum between the spider or strider and the water, which must accompany propulsion (satisfying the law of conservation of momentum: Dickinson et al. 2000), was not known. [Although insects and spiders are not particularly closely related (Regier et al. 2010), it is likely that their water-surface locomotion can be understood in many of the same ways, at least concerning rowing.]

4.2.1 Rowing: With respect to rowing, two hypotheses were in play in the mid-1990s (Fig. 4), neither necessarily to the exclusion of the other. Denny (1993) noted that any object moving at the water surface must create a bow wave if the object's velocity exceeds about 0.23 m/s, the lowest speed at which a wave, responding to the restorative forces of gravity and capillarity, can move. He reasoned that a strider's leg tips, moving backward faster than the wave minimum, would produce a bow wave against which it would push or gain purchase (Fig. 4, bow wave). The wave's sternward motion would contain the sought for momentum corresponding to the strider's forward motion.

Vogel (1994) proposed, in contrast, that the resistance provided by the water arises out of a distortion of the dimple's shape—when the leg is at rest, the dimple's net resistance is vertical, but when the leg is in motion, the associated dimple's leading (toward the strider's posterior) surface is more strongly curved than its trailing surface, and the net surface tension resistance points toward the spider's anterior. This hypothesis did not directly address the question of momentum transfer, but it did reflect the certainty that, whatever else was happening, the points of contact between spider or strider and the water surface were located at the cusp of the dimple. Thus, an asymmetry in the surface tension vectors had to be part of the explanation (Fig. 4, surface tension asymmetry).

Three years later, Suter et al. (1997) reported on a series of experiments with fishing spiders, *Dolomedes triton*, that revealed the following: a) as leg velocity increased in the range of 0 to 0.2 m/s, the drag caused by water flowing around the leg and its attached dimple increased rapidly, providing on the order of 85% of the resistance force experienced by the leg; and b) as surface tension was experimentally decreased, small changes in resistance forces were detected, indicating a persistent but still secondary role of surface tension in horizontal propulsion. From a), it followed that a bow wave need not be present to allow water-surface propulsion, a conclusion that removed the paradox identified by Denny (1993, 2004), namely, how could juvenile water striders (and fishing spiders), with leg tip velocities consistently < 0.23 m/s, propel themselves across the water surface in the absence of bow waves? Drag appeared to be the answer. [A core premise of Denny's paradox (Denny 1993, 2004), that waves cannot be generated by objects at the air-water interface that are moving at velocities < 0.23 m/s, has since been falsified for objects moving impulsively or in arcs or circles, as do the propulsive legs of spiders and water striders (Bühler 2007; Chepelianskii et al. 2008; Closa et al. 2010).]

Thanks to further work by Bush and Hu and their colleagues (Hu et al. 2003; Bush and Hu 2006; Hu and Bush 2010) and to Gao and Feng (2011), on water-surface locomotion in water striders and others, we have a nearly complete picture that is both theoretically and empirically grounded.

When an adult water strider or fishing spider sweeps its propulsive legs backward, usually first shifting its weight so

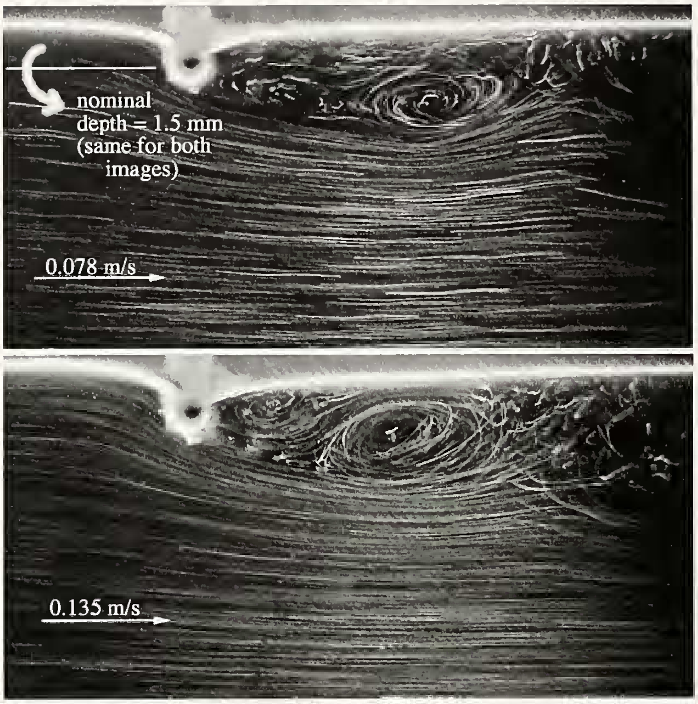

Figure 5.—Particle image velocimetry (PIV) revealing the motions of water during a steady state experiment in which water at constant velocity flowed past a stationary hydrophobic model of a fishing spider's leg. Especially in the lower panel, both the bow-wave and the dimple asymmetry are visible. In both panels, vortices can be seen forming and being shed downstream of the model leg.

that the weight is borne primarily by the propulsive legs, the accompanying dimples deform. The deformation is of the form depicted in Figs. 4 & 5 and results in a resistive force, due to surface tension, that has a net forward-pointing horizontal component. This force opposes the backward motion of the leg and provides the purchase needed for the spider to achieve forward motion. The resistive force is applied to the spider's leg along the perimeter of the area of interaction between the leg and the water surface. Recent experiments have revealed that bending of the long, slender legs of water striders can alter the biomechanical interaction of the leg as it forms a dimple in the water surface (Ji et al. 2012), a detail that may be less important in fishing spiders because of their proportionately stiffer legs.

The cause of the dimple's deformation, in turn, is the water's mass- and viscosity-related resistance to flow, with the mass-related resistance being predominant (Gao & Feng 2011). But the flow does happen, producing a wave at the leading surface of the dimple and vortices under the trailing surface (Fig. 5)—these waves and vortices account (literally) for the momentum transfer between the animal and the water (Rinoshika 2012).

A second resistive force is also operative in these adult surface-walking animals as well as in their smallest progeny, a force neither anticipated in the earlier models of Denny (1993) and Vogel (1994) nor in the studies of Suter and his colleagues (Suter et al. 1997; Suter and Wildman 1999; Suter & Gruenwald 2000a). It is now clear that nanoscale interactions between the strider's leg hairs and the water surface (Feng et al. 2007) have magnitudes large enough to contribute substantially to the resistance experienced when the animal sweeps its legs backwards, "brushing" the water surface (Hu and Bush 2010). Moreover, this "brushing" is anisotropic, meaning that it is directionally asymmetrical. With hydrophobic hairs anchored proximally on a propulsive leg and lying approximately parallel to the leg's surface, the leg meets more resistance when the net direction of water motion is up the leg, and meets less resistance in the opposite direction (Prakash & Bush 2011). This anisotropic "brushing" also makes it less energetically costly to pull the leg from the water surface at the end of a rowing stroke (Prakash & Bush 2011) or at the end of a galloping stroke (see 4.2.2). This "brushing," in both its isotropic and anisotropic forms, is likely to be the only resistance force available to newly hatched water striders and fishing spiders.

Figure 6.—A fishing spider during galloping, photographed just as its legs were leaving the water after a power stroke.

For a comprehensive but still compact treatment of the issues outlined above, see Hu and Bush (2010). To explore an elegant two-dimensional finite-element simulation of water-surface propulsion by small arthropods, one that largely confirms the work described above, see Gao and Feng (2011).

4.2.2 Galloping: In contrast to rowing, the galloping gait commonly seen in pisaurid spiders (Fig. 6) may not have an equivalent in water striders or other insects, but it does have an analog in reptiles. The basilisk lizard, *Basilicus basilicus* (Corytophanidae), runs across the water surface using what has been called a slap and stroke gait (Glasheen and McMahon 1996a, b; Hsieh 2003; Hsieh and Lauder 2004). This involves pushing each hind foot downward fast enough to sharply impact the water surface (the slap), then following through and thereby transitorily opening an air-filled cavity in the water (the stroke), and finally withdrawing its foot before the cavity collapses.

A fishing spider also uses a downward and then backward stroke (Gorb and Barth 1994; Suter and Wildman 1999; Hu and Bush 2010), which briefly opens an air-filled cavity, and then withdraws its legs in preparation for the subsequent stride. The hydrophobicity of the spider's integument (see 4.1.2), however, means that the resistance to the "slap" has both inertial and surface tension components (Hu and Bush 2010), whereas in the lizard, resistance to the slap is entirely inertial [this sets the spiders apart from the lizards with respect to their inclusion in a class of processes called Froude mechanisms (Aristoff et al. 2011), a subject that is interesting but is beyond the scope of this review]. In both cases, the slap phase and the first part of the stroke phase do the work against gravity, elevating the animal, and the latter part of the stroke phase provides the horizontal propulsion (Glasheen and McMahon 1996a; Suter and Wildman 1999; Hu and Bush 2010).

At the end of bouts of rowing and galloping, water-walking spiders are slowed by the same forces that offered resistance to the propulsive strokes that got them moving in the first place — the horizontal component of the net surface tension vector due to dimple deformation, and the micro-scale drag forces encountered as the spiders' leg and body surfaces brush the water surface (see 4.2.1). In addition, during shore-initiated predatory attempts, fishing spiders may grasp their own dragline silk, previously anchored to solid substrate on shore, thereby bringing themselves to a rapid stop (Gorb and Barth 1994).

4.2.3 Jumping & sailing: Spiders that frequent the water surface sometimes take advantage of its peculiar properties (see 3.1.1) in ways that do not quite fit the definition of active locomotion but should be mentioned here nevertheless: jumping and sailing.

The vertical jumps from the water surface performed by fishing spiders (Suter and Gruenwald 2000b; Suter 2003; Hu and Bush 2010), and probably by other lycosoid spiders, involve all eight legs. The spider, which is initially splayed on the water surface, simultaneously and forcefully depresses its legs, producing with each leg the same kind of slap and stroke motion that is characteristic of the spider's legs during galloping. In this case, though, the horizontal forces caused by the legs' movements approximately cancel each other, resulting in a vertical leap but little horizontal displacement.

In the contexts of function and fitness, these vertical jumps are unlikely to reduce mortality due to attacks by fish from below (Suter and Gruenwald 2000b), but are quite effective in evasion of attacks from the side by frogs (Suter 2003). In the latter situation, the necessary and sufficient trigger for the vertical jump was shown to be the compression wave front that precedes the attacking frog, detected by the spiders' leg-borne trichobothria. Attacking spiders, either on the water surface or on land, also are preceded by that kind of compression wave front, potentially rendering them detectable by their intended prey (Casas et al. 2008).

As discussed above, spiders with strongly hydrophobic surfaces, at rest, have a relatively tenuous physical contact with the water surface. This presents problems for active locomotion but facilitates passive displacement when a breeze is present. An entirely passive (prone, legs and body in contact with the water surface) water-borne spider would experience some air movement close to the water, but would be pushed along relatively slowly. This is because air velocity at the surface, at the base of the local boundary layer, would be substantially lower than the velocity just a few millimeters above that (Denny 1993).

Fishing spiders, and perhaps other lycosoid spiders, often either elevate their forelegs (Deshefey 1981) or raise their bodies by standing on the tips of their tarsi (Suter 1999) when on the water surface in a breeze. These postures, called sailing, take advantage of the increased air velocities found higher up in the boundary layer. However, as is the case with ballooning (e.g., Reynolds et al. 2006), there appears to be little opportunity for sailing spiders to affect their direction of motion.

5. SUMMARY

Many spiders have hydrophobic surfaces that allow them to remain dry on the surface of a pond or stream. Among these, some can achieve coordinated and effective locomotion on that air-water interface despite their tenuous contact with it. A few groups of spiders have evolved specialized gaits, different from those used on solid substrates, that appear to be adaptations to locomotion on the water surface.

Empirical and theoretical research during the last two decades has revealed many of the morphological, biomechanical and fluid dynamic components of the rowing locomotion that allow some spiders, like fishing spiders, and some insects, like water striders, to inhabit that habitat preferentially. The central questions addressed by the research have concerned how water-walking arthropods achieve propulsion. The answers are interesting: 1) when at rest on the water surface, a spider's or water strider's weight distorts the water surface, forming a dimple wherever the weight is borne; 2) the backward sweep of a leg and its dimple distorts the dimple, thereby causing the sum of the two vectors of surface tension (one along the leading edge of a leg, the other along the following edge) to have a forward component, thus offering resistance to the animal's backward push; 3) at the same time, the leg-cum-dimple acts as an oar blade, pushing water backward and the animal forward; 4) also at the same time, and probably especially important for early instar fishing spiders and water striders, hydrophilic parts of the ventral surfaces of the legs (not yet demonstrated in spiders) are in intimate contact with the water surface, and their backward motion encounters drag resistance; and 5) the forward momentum that the arthropod achieves is matched by the momentum of backward-moving vortices of water. To some extent, these same components are operative in the less common forms of water locomotion that include galloping, jumping and sailing.

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